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DIURNAL MOVEMENTS AND DISCHARGE CHARACTERISTICS OF ELECTRIC GYMNOTID FISHES IN THE RIO NEGRO, BRAZIL

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Fishes of widely differing evolutionary backgrounds possess organs specifically adapted to produce an external electric field. In most, the field produced by the electric organ is too weak to be of use as a weapon, hence the name "weakly electric fish," to distinguish them from the strongly electric freshwater electric eel (*Electrophorus*) and electric catfish (*Malapterurus*) or the marine *Torpedo* and Stargazers (Family Uranoscopidae) (Lissmann, 1951; Coates, 1947, 1954).

Lissmann and others have shown by behavioral tests that *weakly electric fishes* can detect changes in the conductivity of their surroundings (Lissmann, 1958; Lissmann and Machin, 1958; Machin and Lissmann, 1960; Wantanabe and Takeda, 1963). This is accomplished by using the electric organ as the energy source, and specialized cutaneous receptors as the receivers for a system of active electrolocation, although the actual mechanisms involved are different than first suggested (Machin and Lissmann, 1960; Bennett, 1967).

Both the structure and the physiology of the electric organ and the receptors have been studied in several *weakly electric fishes* (reviewed by Bennett, 1961, 1967, 1968). Yet despite experimental evidence showing that *weakly electric fishes* are capable of utilizing their unique sensory system, little research has been performed to determine the extent to which their usual behavior depends upon use of this system (Lissmann, 1961a, b). This article reports studies of weakly electric gymnotids.

Fishes were captured and studied in aquaria on board the R/V Alpha Helix. The movements of fishes in the river were followed by recording their electric discharges.

Study Area

The R/V Alpha Helix moored at 01°24 S, 61°27 W, downstream of the confluence of the Rio Branco and the Rio Negro rivers about 200 miles north of Manaus, Amazonas, Brazil. This point was about 160 m from an island near the right bank of the river. Average river width exceeded 1 km, and the average rate of flow at the ship was 0.59 knots (measured on May 5–7, 1967). Surface water temperature was about 28°C. Water near the right bank, of Rio Negro origin, was free of sediment but the color of weak tea; it will be called "black water" following common usage. Near the left bank, sediment filled water from the Rio Branco predominated; this will be called "white water." Fine sand and mud overlain with sunken leaves and branches, and occasional clusters of boulders, comprised the river bottom. An area near the right bank was studied most intensively. Varying sized spotches in Figure 1 appearing to be bushes growing along the right bank of the river were in fact large and small trees standing in water 6 m deep. River depth near the ship was determined with a portable Bendix echo sounder. By local report, the river undergoes a depth change of about 6 m annually, and much of the study area was usually above water during the dry season. During the study, 4 April to 15 May 1967, the river was approaching flood stage, and the forest surrounding the base camp on the island was covered with water.

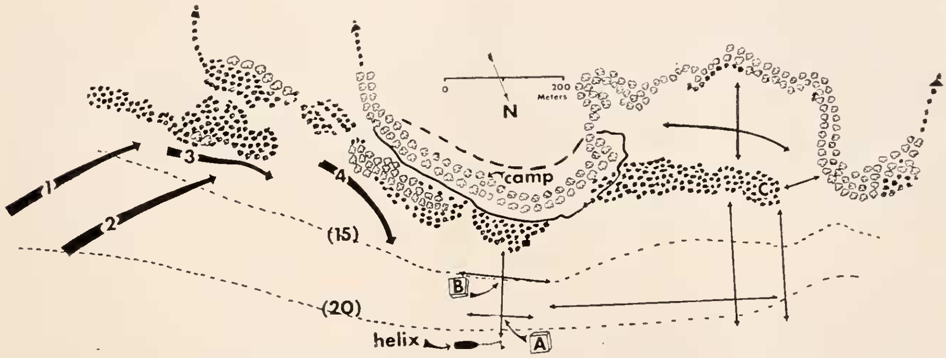

FIGURE 1. Sketch map of the study area; "helix" denotes the R/V ALPHA HELIX anchored off an island on the right bank of the Rio Negro. The large and small splotches denote large and small submerged trees. Dry areas are shown by solid and dashed lines around the camp area. Heavily dashed arrows indicate continuations of the submerged trees and the island proper. The lightly dotted lines indicate approximate depth contours in meters. The large solid arrows (1–4) denote trawling locations. The thin lines mark locations where transects of activity were made. The boxed letters A and B show the location of marking buoys. Magnetic north and a scale of distance are noted.

METHODS

Electrical activity from fishes was detected by recording between two carbon electrodes fixed 0.4 m apart attached to a 26 m coaxial cable marked in 1 m gradations. Signals were amplified by a miniature transistor pre-amplifier and earphone (called "fish detector" henceforth) or recorded on magnetic tape with a Sony portable A.M. recorder. To obtain transects of activity *versus* position, these electrodes were dragged slowly behind a canoe over bottom transects. Tape recordings made during these transects were later integrated electronically (1 to 5 sec time constant). The integrated record was plotted out on a XY plotter as a function of time; by paddling at a constant speed over a known distance this procedure provided a record of activity *versus* position. This method weighted sinusoidal signals preferentially to pulsed signals, and thus could not be used to make quantitative comparisons between different species of fish. Identifications of pulse shape and frequency were made from original tape records with a Tektronix 502A oscilloscope.

Activities at two fixed locations were sampled at various intervals for several days and converted to numerical levels of integrated activity, for quantitative comparison. Other measurements of activity, of a less quantitative nature, were made by noting the amplitude of the signal heard with the fish detector. In controlled tests, fishes could be detected within a radius of about 2.5 m. Because signal strength varied with species, distance, and position of the emitting fish, no attempt was made to determine positions of individuals within this sampling radius. One or two fish could be distinguished from many individuals.

Gymnotids were found only under thick cover (shallow water) or at some depth, and were never seen underwater. They were collected with a 4 m otter trawl towed along the bottom, behind a power boat at a speed of about 0.5 knots. Trawls were made at various hours of the day and night, usually along the lines indicated by the heavy black arrows (labeled 1 to 4) in Figure 1. Fishes were observed in aquaria on board ship. Using an electronic counter, the exact frequency of discharge was determined for several individuals of each major species. Rough "maps" of the electric field produced by each specimen were made with a monopolar electrode, and the types and locations of electric organs were determined by dissection of fresh and formalin fixed specimens.

Observations

Collection and examinations of specimens

Several trawls were made along each of the tracks indicated (Fig. 1). The total catch composition, by species, is given in Table I, column 2, and was proportionally the same in all trawls. Pending a revision of the gymnotids, species designations follow Ellis's key (1913; see also Eigenmann, 1922; Schultz, 1949). During daylight hours (roughly 0600 to 1800 hrs) many fishes were caught trawling along tracks 1 and 2 (in deep water) and less than 5 per trawl along tracks 3 and 4 (near the shore). At night less than 6 fishes were trawled along tracks 1 and 2, while about 30 per trawl were caught along tracks 3 and 4.

Fish of a given species always showed the same waveform of discharge. Fish in group 2 (Table I, column 7) could change their frequency (but not waveform) of discharge when disturbed (Lissmann and Schwassmann, 1965; Mandriota, Thompson and Bennett, 1965; Wantanabe and Takeda, 1963); this was observed in aquaria and under natural conditions. With one exception, all other fish discharged at a constant frequency (Lissmann, 1958; 1961b). Individual black *Sternarchus* specimens were capable of abrupt transient increases in frequency, producing an audible chirp in the fish detector (Yoshika Oniki, Instituto Pesquesas Escola Agronomica Nacional, I. P. E. A. N., personal communication; Bullock, 1970).

Species could not be identified reliably by electrical criteria. Considerable overlap in ranges of discharge frequencies was observed (Table I, column 5), and waveforms of discharge were the same for 4 species (Group 1, Table I). For the 13 species examined, electrical criteria alone suggested 6 "groups" of fishes (Table I, column 7, Fig. 2). In all cases increase in temperature increased discharge frequency (Enger and Szabo, 1968). The range of body length for each species is noted in Table I. There was no correlation between body length and frequency of discharge.

TABLE I

Numbers of Gymnotids of various species and their size, and frequency of discharge. The fishes are also grouped according to frequency range and waveform of discharge

Species	Fish		Discharge frequency		Body length range (cm)	Group*	Discharge frequency range	Per cent† tot. sig.
	Caught	Studied	Mean	Range				
Sternarchella sp.	410	26	1200	932–1384	8–15	1	900–1300	40
Adontosternarchus sp. (var.)	372	21	1036	889–1241	6–10			
Sternarchus sp. (black)	58	12	1134	964–1466	13–16			
Adontosternarchus sp. (black)	20	8	1184	1053–1330	6–10			
Steatogenys sp.	219	15	55	40–70	7–15	2	35–80	35
Gymnorhamphicthys sp.	2	2	40	18–55	10			
Rhamphichthys sp.	2	1	40	20–55	10			
Eigenmannia virescens	19	5	320	300–360	10–15	3	300–800	10
Eigenmannia macrops	13	8	750	725–802	8–12			
Sternarchorhynchus sp.	17	8	1268	1020–1702	10–20	4	1100–1700	5
Sternarchorhamphus sp.	17	8	920	740–973	13–35	5	800–1000	5
Sternopygus-like (rough)	7	2		104–165	15	6	100–200	5
Sternopygus-like (smooth)	2	2		100–150	10			

* Number designations of groups are arbitrary. Fish were grouped by analysis of both frequency and waveform of discharge.

† Figures are estimated percentages of the electrical signal detected in the river that could be clearly identified as originating from a given group of fishes. The frequency range of discharge given for each group is based on analysis of tape recordings taken from the river.

There were considerable differences in behavior within the group of fishes having virtually identical discharge characteristics (group 1). For example, although the fish called black *Sternarchus* sp. aggregated in aquaria, individuals showed extreme intra-specific interaction, probably aggressive, manifested by approaches, bumping attacks and chasing (Yoshika Oniki, personal communication). In aquaria these fish showed some interest in black *Adontosternarchus* sp., a smaller fish with a very similar waveform and frequency range of discharge, but

TABLE II

Electrical activity recorded with the fish detector at various locations underwater within three miles of the ship anchorage. Intensity of activity is denoted by one or more plus signs (+) and no activity by a zero (0), while no or insufficient data are indicated with a bar (—). Night time activity along the left bank was not studied.

Location	Depth (m)	Right bank		Left bank
		Day	Night	Day
Small streams and inlets	0–4	+	—	+
Flooded trees	2–6	0	0	+
Backwater channels	6–20	0	0	++
Perimeter of trees	6	0	+++	0
River near trees	6–10	0	+	—
River main channel	10–20	++	0	++

did not engage in the displays observed between two black *Sternarchus* sp. The black *Adontosternarchus* sp. were not aggressive, and were generally less active than the black *Sternarchus* sp.

In aquaria, all of the fishes tended to gather together in species specific aggregations to some extent. *Steatogenys* sp. formed particularly close aggregations, with no apparent intra-specific aggressiveness, and showed a clear day-night activity cycle, preferring to hide under available cover during the day. They comprised the major part of group 2 (Table I).

TABLE III

Comparisons of intensities of electrical activity obtained by sampling in four areas during the day and night (Fig. 1). Each number is the average intensity recorded during a one minute period with recording electrodes on the bottom. The arbitrary scale 0 to 5 was derived by calibrating the gain adjustment on the fish detector and is not the same as the scale shown in Figure 5.

Depth and location in Figure 1.	Activity (scale 0 to 5) during hours 0900–1700	1700–0600
16 meters	4, 3, 1, 1, 3, 2	0, 1, 1, 1, 1
Right hand side	3, 1, 1, 2, 1	2, 0, 0, 0, 0
16 meters	4, 3, 1, 1, 3, 2	0, 1, 1, 1, 1
Right hand side	3, 1, 1, 2, 1	2, 0, 0, 0, 0
12–18 meters	5, 5, 2, 3, 5	0, 0, 0, 1
Right middle		1, 2, 0, 3, 0
18 meters	2, 3, 3, 2, 2	0, 0, 0, 1, 1, 0
Left hand side	1, 1, 3, 1	0, 2, 1, 1, 1, 1
6 meters	0, 0, 0, 0, 0, 0	5, 5, 4, 3, 5
Along trees		4, 5, 3, 3, 5

Each trawl took about 10 minutes, and although little debris was picked up, the net obviously damaged many specimens. The most numerous species (variegated *Adontosternarchus* sp. and *Sternarchella* sp.) had the highest mortality rate; less than 30% of each catch survived for more than 2 hours after capture. The stomach contents of all species were rather similar, although *Sternarchella* sp. usually had a quantity of fine sand in the stomach that was not found in the other species. Insect larvae, isopods, filamentous algae, and portions of unidentifiable exoskeletons were found in all stomachs. Stomach contents were larger and better preserved in fish collected in the early morning, which would support a hypothesis of nocturnal feeding.

Of the 13 species collected and examined by dissection (species represented by a single specimen are not listed) those in groups 2, 3 and 6 (Table I) had electric organs of muscular origin (Szabo, 1966; and review by Bennett, 1961), while those in the other groups had organs derived from nerves (Oliveira-Castro, 1955; Bennett, 1966). Thus as a rule low frequency fishes have organs linked to spinal neurones by a chemically transmitting synapse, while the organs of high frequency fishes are themselves modified spinal neurones. In all cases the main electric organ or organs were located primarily in the posterior part of the body, some-times extending forward to a point anterior to the visceral cavity (Bennett, 1961, 1968). Fish in group 2 had auxiliary organs also of muscular origin in the head (Bennett, 1962).

Localization of electrical activity

Table II summarizes the intensities of electrical activity recorded with fish detector at various locations underwater in or near the main river. No activity was ever detected within the flooded (igapo) forest along the right bank. Low frequency activity was detected within the igapo forest along the left bank. Only low frequency activity was detected in small streams and inlets and single specimens of *Hypopomus* sp. and *Steatogenys* sp. were captured there. Much of the daytime activity detected in deep water, and also along the submerged lines of trees

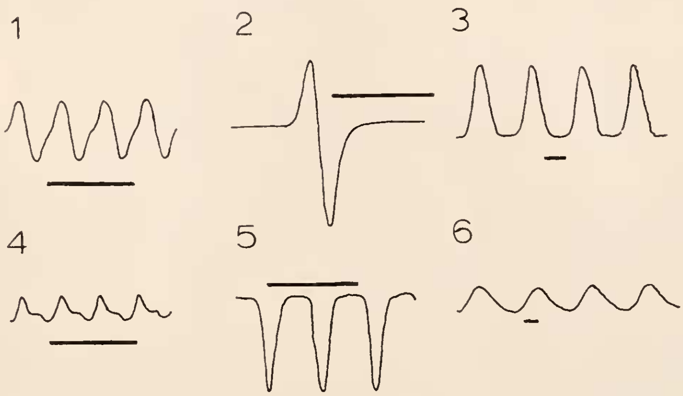

FIGURE 2. Characteristic waveforms of discharge for groups of fishes (Table I). Recordings were made with a monopolar electrode placed near the head; a head positive deflection is upwards. A time calibration bar indicates 2 msec (1 msec for waveform 2); the maximum signal detected was about 50 mV.

at night, was high frequency (Table I, column 8, 9). On a basis of frequencies and waveforms of activity, 6 groups of fishes were identifiable, corresponding to the six groups of electrically distinct fishes studied in aquaria (Table I, column 7).

Table II indicates that locations where activity was highest during the day became silent at night, and vice-versa. Activity during the day in deep water appeared to be concentrated in patches, although always at or near the bottom. At night, activity was spread continuously along the tree line, from about 1 m to the bottom (Table III).

Particularly intense patches of daytime activity were found just inshore from the ship anchorage (Fig. 3). A rocky area extending underwater from the shore probably provided secure resting places for the fishes. Transects of activity were made across this area at various times of day and night on a total of five days. Typical results for a transect made on four occasions from near the ship mooring towards the shore are depicted in Figure 4. The second, third, and fourth traces, taken during daylight hours, indicated two roughly constant patches of

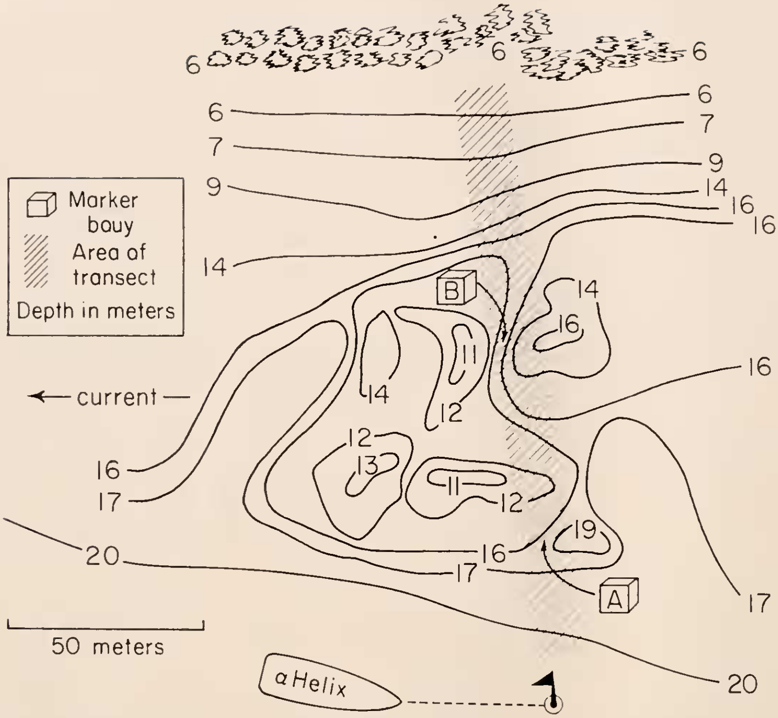

Figure 3. Depth contours of the river bed inshore from the ship anchorage. The steep drop-off from 6 to about 15 meters and the drop at 20 meters are typical of the river as a whole; the irregularities shown indicate the rocky submerged point extending from the shore (the line of submerged trees is indicated by splotches). The path taken during the transects illustrated in Figure 4 is shaded.

activity. The type of activity is indicated by a number (referring to the groups in Table I) below each trace. Artifacts (subscripted "A") resulted when the electrodes truck rocks. The lowest trace (heavy line) indicates depth along the transect. Practically all activity along the entire transect vanished during the night (compare the upper trace with others; the recording gain was about 10 times that used in the third trace, and 5 times that in the second and fourth traces). Thirteen other transects (not illustrated) along the lines shown in Figure 1 indicated that activity was restricted to patches, and was not distributed along the river bed at a constant depth or distance from shore.

To determine the stability of the deep water activity, two anchored buoys (marked A and B in Figs. 1, 3 and 4) were placed over areas of high daytime activity, and integrated bottom activities below these buoys were determined at intervals (Fig. 5). During the day, activity at buoy A was emitted exclusively by group 2 fishes, while that at buoy B was a mixture of groups 1 and 3. On successive days, activity at buoy A was constant to within at least ±10%, while that at buoy B was slightly more variable, ±25%. Each aggregation was found to be about 3 m in radius. Between 1600 and 1800 hrs, as the sun set, activity began

FIGURE 4. Transects of electrical activity versus position (date and time as noted), taken along the path indicated in Figure 3 and plotted by the method described in the text. Net gain of the electronic apparatus used was 5 times higher in the first trace than in the second and the fourth, and 10 times higher than in the third. The numbers under activity peaks refer to identified groups of fish (Table I). Artifacts are indicated by the letter A. The heavy line trace shows in depth in meters. In each case the distance covered was about 140 m, but during the uppermost trace paddling speed was slower, and thus the trace is somewhat longer. It may be seen that the major peaks of activity appear in the same places at all times, and that at night virtually all activity is lost.

to decrease at buoy A. At buoy B, activity of group 1 and 3 lessened, but was replaced, towards 1900 hrs, by activity of group 2. After 2000 hr activity declined at both buoys, and by 2100 hr what little remained consisted of a mixture of all groups (mostly single specimens) at buoy A and group 1 and 2 at buoy B.

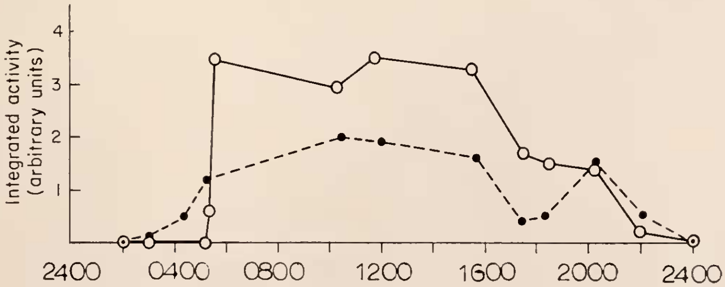

FIGURE 5. Plot of integrated activity in arbitrary units versus time in hours for one twenty four hour day. Each point indicates one measurement; the solid lines and open circles O——O record activity at buoy A and the dashed lines and filled circles (●---●) that at buoy B (Fig. 3).

By 2400 hrs there was essentially no activity at either buoy. Single fish were detected at both buoys on some occasions. Near the submerged trees, activity reached a maximum at about 2300 hr and remained at a high level (all groups intermixing) until about 0430 hr. At about 0500 hr a mixture of all groups of activity was usually detected at buoy B, but nothing at buoy A. Within about 20 minutes the activity at buoy A had reached daytime level.

Discussion

More than 1000 gymnotids were trawl collected, representing at least 13 species. Because of overlaps in frequencies of electrical discharge and also similarities in waveform of discharges, only 6 groups were distinct using purely electrical criteria. The same 6 electrical groups were identified from analysis of activity recordings made under natural conditions. It seems probably that the species studied in aquaria fairly represent the species studied under natural conditions. The percentage of total activity attributable to each group in recordings made under natural conditions was about the same as the percentage composition by a group of the fishes collected in trawls.

Electrical activity was intense in deep water and absent along the shore during the day. Fishes were plentiful in deep water and scarce in shallow water during the day as indicated by numbers caught in trawls. With regard to both electrical recordings and trawling this situation reversed at night. These observations support the belief that electrical methods were of value in following the diurnal movements of the fishes.

The fishes studied resemble those previously reported by others with regard to body form, origin and location of electric organs, and waveform and frequency of electrical discharges (see Lissmann, 1958, 1961b; Bennett, 1961, 1968). It is interesting that fishes of different species whose electrical characteristics appear to be identical can quite clearly recognize members of their own species. Presumably not only the electrical discharges but the changes in discharge waveform as a fish moves are important in species recognition, just as movements (displays) are important to visually oriented animals.

Fish belonging to group 2 (probably *Steatogenys* sp.), aggregating at buoy A, made diurnal migrations over a distance of at least 100 m, and from a depth of about 16 m to the surface along the tree line. There was no reason to believe that the fish left the bottom in midstream. They might have navigated either by smell or by feel. However, electrical recordings from fixed locations indicated that the same or an equivalent number of fish returned to the same spot day after day within a very short time period each morning. Since the fishes dispersed at night along the trees, they apparently have an ability to reaggregate as well as to navigate over relatively long distances. Electroreception is not the only sense that could produce this ability, but it would certainly be of use under the conditions in which the fishes live. The constancy of activity during the day near buoy A suggests that the fish remained quiescent; this was supported by aquarium observations of *Steatogenys* sp.

Both high and low frequency fish were found throughout the study area near the main course of the river, and apparently shared the same feeding ground at night. The high frequency fishes were more abundant in the river (Table I), and were not found in the shallow waters along either bank. No gymnotids were found in the semistagnant black water in swamps along the right bank, perhaps because there was little food available in this water. The fish studied were smaller than those of the same or similar species studied elsewhere (Ellis, 1913), again perhaps because of the low nutrient content of black water.

Lissmann (1961b) found using electrical recording in the field that gymnotids near Belem, Brazil living in relative shallow clear water dispersed from daytime hiding places among rocks, weeds or trees and became active at night. This behavior would effectively avoid visually oriented predators (Lissmann, 1961b). In the present study, potential predators were not captured in trawls. The gymnotids captured had small mouths and teeth. Possibly predation becomes significant only during low water when, by local account, electric eels, piranhas and many other potential predators frequented the study area. Captive electric eels avidly pursued and consumed weakly electric fishes and appeared to be homing in on the electric signal during pursuit as evidenced by increased average time required to catch spinalized fishes lacking electrical discharges. Electric eels respond behaviorally to electrical signals, and possess electroreceptors similar to those of other gymnotids (Hagiwara, Szabo and Enger, 1965). However, the failure to catch predators in the trawl may simply reflect inadequate methods.

The extreme annual changes in water level may partially explain the diurnal movements of the gymnotids. During the dry season, most of the vegetation shown in Figure 1 would be on dry land. The fishes may choose to maintain resting places in water that does not disappear seasonally, rather than simply moving with the changing waterline.

The movements of the fishes studied, and their species specific daytime aggregating tendencies do not, of course, prove that the fishes use electroreception for either navigation or species recognition. However, because of the opaque, deep water in which the fishes live, it is obvious that their known electrosensory abilities would be of considerable advantage. The extent to which electroreception actually determines behavior is a question that remains for more controlled experimentation to answer.

I am especially indebted to Captain Faughn and the crew of the Alpha Helix for their help, to members of the scientific party for their suggestions and criticism, and to the National Science Foundation for supporting the 1967 Ouro Verde Amazon expedition. I also wish to thank The Rockefeller University, at which I was a student, for a travel grant and for the loan of equipment.

Summary

Gymnotids of 13 species were trawled in water 10–20 m deep; all emitted weak electrical discharges. Each fish had a typical frequency of discharge; each species had a typical range of frequency but there were overlaps between species. Waveforms of discharge were similar in several species. Electric organs were derived from muscle tissue in most low frequency species and from nerve tissue in high frequency species. Diurnal movements of fishes were followed electronically.

Fishes formed aggregations in 15–20 m deep water about 100 meters from shore during the day and dispersed along the shore at night. Individual daytime aggregations were re-established each morning.

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